



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

BULLETIN
OF THE
TORREY BOTANICAL CLUB.

Vol. XVIII.] New York, March 10, 1891. [No. 3.

A Study of the Apical Growth of the Prothallium of Ferns with Reference to their Relationships.

BY DOUGLAS H. CAMPBELL.
(Plate CXV.)

In January of last year I published in the *Botanical Gazette** a paper on the affinities of the Filicineæ suggested by a similar one by Bower† in the *Annals of Botany*, the object of my paper being to defend the older theory of the origin of the ferns from the Hepaticæ, as opposed to the later theory of Bower‡ and others that the ancestral forms of the pteridophytes were alga-like forms similar to the filamentous prothallium of certain Hymenophyllaceæ which are regarded as the most primitive of living Filicineæ.

Having been engaged for some time past in the further study of this problem, a number of facts have been collected which may serve to throw some further light on this most interesting question.

As is well known, the prothallium of most ferns bears a most striking resemblance to certain thallose liverworts,—indeed, so striking is the resemblance that sometimes a microscopic examination is necessary to distinguish them, and when the prothallia remain unfertilized they may reach a size considerably surpassing many of the smaller liverworts.§

In its earlier stages the young fern-prothallium usually grows

* Campbell—On the affinities of the Filicineæ. *Bot. Gaz.* Jan. '90.

† Bower—The Comparative Examination of the Meristems of Ferns as a Phyto-genetic Study. *Annals of Botany*.

‡ Bower—I. c. p. 386.

§ Goebel—"Outlines." p. 199.

by means of a single two-sided special cell, which is often established very early (See Fig. 1-a), and may persist until the prothallium has reached a considerable size. This cell has two sets of segments cut off from its sides, by walls which are parallel to the latter. This regular succession of segments is usually conspicuous and the limits of the individual segments are often recognizable for a long time (Fig. 2). Sooner or later the apical cell is divided by a wall at right angles to the axis of the prothallium into a marginal cell, four-sided when seen from above; and an inner triangular cell (Fig. 6). The former of these next divides in most cases by a longitudinal wall into two equal cells, but in some cases observed (in *Osmunda cinnamomea*) the single four-sided cell may persist for a time as a single apical cell. (Figs. 4, 5).

All of these points are readily made out from surface views of the prothallium, and with the exception of the last mentioned, have been repeatedly observed and recorded by numerous writers; but the fact that in the later stages of the apical cell (or cells), there is a perfect regularity in the succession of segments cut off, seems to have entirely escaped the attention of these investigators. Kny* it is true, figures, in the main correctly, a longitudinal section of the prothallium of *Osmunda regalis*, showing the apical cell and its younger segments; but makes no reference to having detected any regularity in the arrangement of the cells, simply stating that walls are formed parallel to the surface of the prothallium, thus giving rise to the thickened midrib characteristic of the prothallium of the Osmundaceæ.

When we compare the process of growth here briefly outlined with that of the thallose liverworts, we cannot but be struck with the remarkable resemblances—nay, identity in many cases—of the two.

The liverworts have been repeatedly and carefully studied, especially by Leitgeb, and in his magnificent work† upon them, we have ample means for comparing their development with that of the fern-prothallia. Recently also, Kny‡ has published an

* Kny—Entwicklung des Vorkieimes von *Osmunda regalis*. Pl. II. fig. 2.

† Leitgeb—Untersuchungen ueber die Lebermoose. 1874-1881.

‡ Kny—Bau und Entwicklung von *Marchantia polymorpha*, 1890.

account of the structure and development of *Marchantia* which shows also some remarkable resemblances to the growth of the fern-prothallium. So often, indeed, in comparing the liverworts with the fern-prothallium, do we meet with the same structure and method of growth, that such extraordinary correspondence of structure, without a corresponding relationship, seems impossible.

Of the liverworts known at present, the thallose Jungermanniaceæ and certain Anthocerotæ approach most nearly in structure in their mature condition, to the fern-prothallium. In the former, according to Leitgeb* there is always a single apical cell so that these plants show throughout their life a condition which is usually but transitory in the fern-prothallium. In such forms as *Metzgeria* too, the structure of the thallus is essentially the same as the prothallium of the Osmundaceæ.

In *Metzgeria* and *Aneurat*† as well as other related genera, the apical-cell is of the two-sided form and the succession of segments same as in the fern-prothallium. In *Pellia*‡ it corresponds closely in form to that shown in Fig. 4, 5, and probably represents a higher degree of development.

In the Anthocerotæ§ there seems to be at the growing points of the full-grown thallus a row of similar cells, much as in the full-grown fern-prothallium. Whether this is preceded by a single apical cell in the young plant is uncertain, as our knowledge of the germination of the spores is limited to that of the genus *Anthoceros*|| and this point does not appear to have received the attention it deserves.

The Marchantiaceæ** and Ricciaceæ,†† correspond closely in the structure and growth of the thallus, and all, so far as is known, have at the growing point a row of similar cells, cutting off two sets of segments above and below. The germination of the spores in the latter group is known only in *Riccia glauca*, and according to Leitgeb‡‡ is entirely similar to that of the

* l. c. Vol. III. p. 6.

† Leitgeb, l. c. Vol. III. p. 40. Pl. I. II.

‡ Leitgeb, l. c. Vol. III. p. 7, 53. Pl. III.

§ Leitgeb, l. c. Vol. V. p. 13. pl. I.

|| l. c. p. 29.

** Leitgeb, l. c. Vol. VI. p. 2.

†† l. c. Vol. II. p. 16. Pl. IX.

‡‡ l. c. p. 23.

Marchantiaceæ investigated. Unfortunately I have been unable to find an account of the details. Of the Marchantiaceæ *Marchantia* has been the subject of a recent work by Kny already cited. This latter is especially interesting, as it shows that in its development the young thallus follows step by step, precisely the same course described in the young fern-prothallium*. First the protonemal filament; next oblique walls cutting off a *single two-sided apical cell*; this is then divided by a transverse wall, and the inter cell, by longitudinal walls becomes transformed into the row of marginal cells that characterizes the growing point of the older thallus.

Owing to their extreme delicacy, it is almost impossible to make satisfactory longitudinal sections through fern-prothallia without imbedding them. It is no doubt for this reason that no satisfactory account of the cell-division in the apex, subsequent to the formation of the thickening back of it, has been given. It is possible, however to imbed them in paraffine and it is then a simple matter to make very thin sections which show every detail of structure with perfect clearness. It is then plainly evident that the divisions are perfectly regular and referable to a type found among the liverworts.

To prepare the specimens for imbedding 1 per cent. chromic acid was used to fix them, and after dehydrating and passing gradually into turpentine, they were placed for several hours in melted paraffine. As a stain, Bismarck brown was the most satisfactory. A solution in 70 per cent. alcohol was used, staining on the slide. In this way the young cell-walls are strongly colored and the preparations show every detail with the utmost sharpness.

SPECIAL INVESTIGATIONS.

Sections were made of the prothallia of *Onoclea sensibilis* and *O. Struthiopteris*, as well as a number of undertermined Polypodiaceæ, and of *Osmunda cinnamomea*. In all of these a strong resemblance was observed.

In the larger prothallia of the Polypodiaceæ, so far as observed, the growing point consists of a row of several cells, (Fig. 3, a, a', a''), each one nearly four-sided as seen in sections parallel with the surface of the prothallium. These divide oc-

* Kny, l. c. pp. 387-389. Fig. xc.

casional by longitudinal walls and thus add to the number of marginal cells of the prothallium; but the further growth of the secondary marginal cells is limited, while that of the apical cells is unlimited. From the bases of the apical cells segments are also cut off, which contribute to the formation of the cushion which bears the archegonia.

Vertical sections of the apical cells are almost perfectly semi-circular in form (Figs. 7, 8, a), and comparing this with the surface view, or sections parallel to the surface, we see that these cells are shaped like a flat half-disk. As compared with the other cells they are large, and an examination of the segmentation shows that the divisions occur with great regularity. The segments are cut off by a wall parallel with the inner wall of the apical cell, and reach from the upper surface to the lower one of the prothallium. (Figs. 7, 8). The segment is next divided by a wall at right-angles to the first formed, into two cells, of which the lower one (the upper one in the figure), is slightly larger, and divides more actively than the upper, so that the thickening on the lower side of the prothallium is more marked than on the upper, and results in the formation of the projecting cushion of tissue upon which are borne the archegonia. These seem to bear a definite relation to the segments. After the first division in the young segment, walls are formed in each semi-segment perpendicular to the surface of the prothallium, thus dividing the segment into four cells, two of which are dorsal and two ventral. One of the latter forms at once the mother-cell of the young archegonium. (Fig. 7 ar.).

In *Osmunda* observations were limited to young prothallia that had not yet formed archegonia, but as in this genus there is a thickened midrib traversing the whole prothallium almost from the first, it was to be expected that the method of growth would not deviate very much from that of the Polypodiaceæ. It is not at all infrequent to find in *Osmunda* (*O. cinnamomea*, and *O. Claytoniana*) that the two-sided apical cell of the young prothallium gives place to a single cell from which three sets of segments are cut off—two lateral and one basal. (Figs. 4, 5). In the cases observed this cell was considerably larger than the individual cells of the apex of the other fern-prothallia studied.

The apical cells are longer than those of the Polypodiaceæ, but closely resemble them. (Fig. 9, 10). The segments are cut off from the base in the same way, and the first wall in the segment also divides it into two nearly equal cells, dorsal and ventral. The subsequent divisions, at least in the younger prothallia, are less regular and there is a preponderance of horizontal walls. (Figs. 9, 10). The difference in the rapidity of cell-division in the dorsal and ventral segments is not noticeable. How this may be in the older prothallia, and what the relation of the archegonia to the segments is, I cannot yet state, but hope soon to have an opportunity of examining this point carefully.

When we compare the longitudinal sections of the prothallia with those of the liverworts, we find that most of the latter differ in one marked respect—viz: that two sets of segments are cut off from each apical cell (when seen in vertical section), a dorsal and a ventral one. This seems to be the case in all Marchantiaceæ* and Ricciaceæ†, and in *Anthoceros*‡; but in *Dendroceros*§, a near relative of the latter, we meet with exactly the same form as in the ferns (Fig. 11); and the single apical cell of *Pellia epiphylla*,|| according to Leitgeb's account is also of the same type, although the nearly related *P. calycina*¶ has an apical cell closely resembling in its method of growth the individual apical cells of the Marchantiaceæ, and according to Hofmeister^o, *P. epiphylla* in its earlier stages has the apical cell of the same form, so that the two types must be regarded as closely related, and possibly interchangeable. It is by no means unlikely that further investigation will show both types in the ferns.

Finally, the independent vegetative existence of the fern-prothallia, and the power of multiplication by branching are characters which they have in common with the liverworts, and this is especially marked in the Osmundaceæ, Gleicheniaceæ and Marattiaceæ, just those groups which in other respects ap-

* l. c.

† l. c.

‡ l. c.

§ Leitgeb, l. c. Vol. V. p. 30. Pl. II.

|| l. c. Vol. III. p. 6. 53.

¶ l. c. Vol. III. p. 7. 53.

^o Hofmeister, The Higher Cryptogamia p. 23. Pl. IV.

proach most nearly the liverworts. In the two former a truly dichotomous branching, apparently entirely similar to that in the thallose liverworts, has been recorded by Goebel* and Jonkman.†

CONCLUSIONS.

From a consideration of the facts presented above, it seems that we are justified in assuming a direct relationship between the Filicineæ and the Hepaticæ. The close correspondence in the development of the two groups, as well as the structure of the thallus in the simpler liverworts, indicates that the two groups have had a common origin, and that the Filicineæ branched off from the liverworts at a comparatively late stage. Probably originating from filamentous green algæ (or possibly flattened forms like *Coleochaete*), the next stage was a delicate heart-shaped form with two-sided apical cell, as in the young fern-prothallium and such liverworts as *Metzgeria* and *Aneura*. A thickened midrib was probably early developed, and in the more differentiated forms the whole thallus became several cells in thickness and in the Marchantiaceæ especially, of considerable complexity.

It is not my purpose to speak of the affinities of the different groups of liverworts here, as that has already been ably discussed by Leitgeb‡. It may, however, be well to consider briefly the relative positions of the ferns, as indicated by a comparison with the liverworts. Of the forms that have been investigated, the prothallia of Osmundaceæ§, and Marattiaceæ|| resemble most nearly such liverworts as *Dendroceros* and *Pellia*, and are probably the most primitive. The Gleicheniaceæ,° resemble the Osmundaceæ, in many respects and are in certain ways a connecting link between them and the Polypodiaceæ, with which the Schizæaceæ closely agree. The Polypodiaceæ, with the Cyatheaceæ, form the end of the homosporous series. The Hymenophyllaceæ seem to be degenerate forms, and our present knowledge would indicate that they branched off pretty low down—possibly between the Osmundaceæ and Schizæaceæ.

* Goebel, *Gymnogramme leptophylla*, etc. Bot. Zeit. 1877.

† Jonkman, La Generation sexuée des Marattiacées, p. 208. fig. 57.

‡ l. c. Vol. VI. pp. 49-53.

§ Kny, l. c. Luerssen (Schenck's Handbuch p. 171.)

|| Jonkman, l. c.

° Rauwenhoff, La Generation sexuée des Gleichéniacées.

Our ignorance of the prothallium of the Ophioglosseæ makes it impossible to determine positively their position, but as stated in a previous paper*, there is strong ground for regarding them as the most primitive of all the Filicineæ.

The greatest difficulty, it seems to me, in establishing a direct connection between the liverworts and ferns, is in the different character of the archegonium, and the spermatozoids. The former is very constant throughout all investigated liverworts and differs in some important features from the same organ in the ferns. The spermatozoids too, are different in the two groups, being uniformly bi-ciliate in the liverworts, and multi-ciliate in the ferns. This latter difference I regard as of great importance, and it is much to be hoped that a thorough investigation of this point in the liverworts will be made, to see whether there are forms that deviate from the ordinary biciliate type.

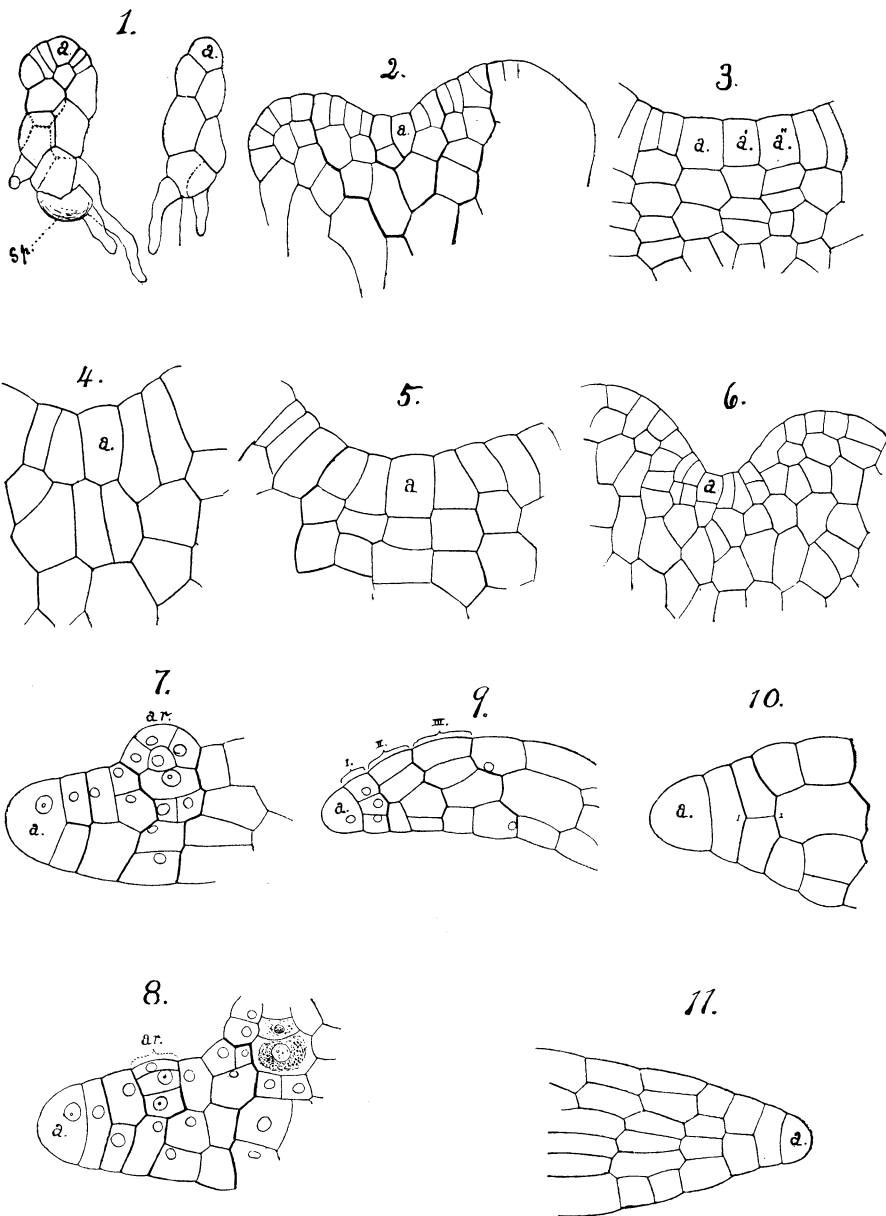
It is by no means impossible that a careful examination of the hitherto unexplored regions of our country, especially the swamps of the Southern States, may bring to light forms which will help to solve the problem of the origin of the Pteridophytes, one of the most important questions, certainly, in systematic botany.

EXPLANATION OF FIGURES.

In all the figures the apical cells are marked a.

- Fig. 1. Two very young prothallia of *Osmunda Claytoniana* $\times 150$. Sp-Spore membrane.
- Fig. 2. Apex of an older prothallium of the same. The limits of the younger segments indicated by heavier lines. $\times 150$.
- Fig. 3. Section of an older prothallium of an undetermined fern (Polypodiaceæ) a, a', a'', the three apical cells $\times 300$. Section parallel with the surface.
- Figs. 4, 5. Two sections parallel to the surface, of prothallia of *Osmunda cinnamomea* with single four-sided apical cell. $\times 300$.
- Fig. 6. Surface-view of a prothallium of the same species, showing the transition from the triangular to the four-sided apical cell. $\times 150$.
- Figs. 7, 8. Vertical longitudinal section of the prothallium of *Onoclea Struthiopteris*, ar. Young archegonia. $\times 300$.
- Fig. 9. A similar section of *Osmunda cinnamomea*; the younger segments are numbered. $\times 150$.
- Fig. 10. Apex of a similar section, with the youngest segment still undivided. $\times 300$.
- Fig. 11. A similar section of *Dendroceros Breutelii* (after Leitgeb). $\times 350$.
- Figs. 1, 2, and 6 are from living specimens; the others fixed with chromic-acid, and sectioned with the microtome.

* Campbell, l. c. p. 3.



D. H. Campbell del.

D. H. Campbell:—APICAL GROWTH OF FERN PROTHALLIA.